

HOST RELATIONSHIPS, ETHOLOGY AND SYSTEMATICS OF  
PSEUDOMETHOCA ASHMEAD  
(HYMENOPTERA: MUTILLIDAE, ANDRENIDAE, HALICTIDAE  
AND ANTHOPHORIDAE)

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*Abstract.*—Two new species of *Pseudomethoca* are described and figured, *perditrix* from Arizona and New Mexico, and *bethae* from Arizona, New Mexico, and the states of Jalisco and Puebla in Mexico; behavioral notes are included for each. Brief taxonomic notes and figures, and/or behavioral notes are given for eight other taxa of *Pseudomethoca*.

*Ps. perditrix* parasitizes larvae of the communal andrenid bee, *Perdita portalis* Timberlake, in New Mexico. *Ps. toumeyii* (Fox) is a putative parasitoid of *Pe. portalis* in New Mexico. The Floridian *Pe. graenicheri* Timberlake may be a host of *Ps. torrida* Krombein. The eumenid wasp, *Ancistrocerus lutonidus* Bohart, is considered to be an improbable host of *Ps. frigida*. *Ps. bethae* was found in Arizona in a nest of the communal anthophorid bee, *Exomalopsis solani* Cockerell. *Ps. mulaiki* Mickel from Texas may have species of the anthophorid, *Exomalopsis*, and/or the halictid, *Agapostemon*, as hosts. *Ps. propinqua* (Cresson) may have as hosts the halictid, *Nomia melanderi* Cockerell, and the anthophorid, *Melissodes pallidisignata* Cockerell in Wyoming. *Ps. sanbornii aetis* (Fox) has the halictid, *Nomia nevadensis bakeri* Cockerell, as a putative host in coastal South Carolina. *Ps. donaeanae* (Cockerell and Fox) has an unknown bee host in Arizona, based on collection of a female bearing numerous pollen grains around the mouthparts.

A table is included of known or putative hosts of *Pseudomethoca* in America north of Mexico and the authorities for each association.

*Key Words:*—*Pseudomethoca*, parasitoid, communal and solitary bees, Andrenidae, Halictidae, Anthophoridae

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There is very little published information on host relationships within *Pseudomethoca* Ashmead. Krombein (1979) listed bee hosts for only 5 of the 44 species-level taxa in America north of Mexico. Manley and Neff (1989) and Riddick (1991) added putative or positive bee associations respectively for two additional species from this area.

There are many additional species of *Pseudomethoca*, mostly undescribed, in Mexico, Central and northern South Amer-

ica. Mickel (1969) and Brooks and Roubik (1983) reported positive bee hosts respectively for one species in Costa Rica, and two more species in Panama.

During the past several years, B. B. Norden and I, working in southeastern Arizona and peninsular Florida, obtained probable or putative bee hosts respectively for one new species and for a previously described taxon. B. N. Danforth, working in southwestern New Mexico, obtained a positive bee association for another new species, and

a putative host association for a previously described taxon. Unpublished putative or probable bee host associations were obtained by A. Hook in southernmost Texas, W. L. Jellison in Wyoming, K. V. Krombein in southeastern Arizona, and D. G. Manley in coastal South Carolina.

Detailed natural history observations and descriptions of the two new taxa, and behavioral and taxonomic notes on previously described *Pseudomethoca* are presented below. A concluding section on host relationships includes a tabulation of 14 species-level taxa, their positive or putative bee hosts, and the authorities for each association.

Depositories for specimens listed are as follows:

AMNH	American Museum of Natural History
DGM	Donald G. Manley, personal collection
DJB	Denis J. Brothers, personal collection
ESB	Eric S. Brewster, personal collection
KU	Snow Entomological Museum, University of Kansas
USNM	National Museum of Natural History, Smithsonian Institution

*Pseudomethoca perditrix* Krombein,

NEW SPECIES

Figs. 1, 3–5, 7, 8

This small species runs to couplet 17 in Mickel's revised key to species (1935). It differs from the two taxa keying out there, *Ps. oculissima* Mickel and *Ps. scaevolella* (Cockerell and Casad), in the edentate inner margin of the mandible (cf. Figs. 1, 2), and the more sparsely punctate and hirsute second tergum (cf. Figs. 6, 7) which lacks the paired spots of recumbent silvery vestiture.

Holotype female.—Length: 4.2 mm. Ferruginous, apex of mandible black, thoracic dorsum anteriorly slightly darker; legs darker

brown except tarsi; head above (Fig. 4) with dense, recumbent, silver pubescence and longer, scattered, erect silvery setae; dorsum of thorax with somewhat coarser and sparser appressed pubescence, black anteriorly, silvery posteriorly, and with longer, erect, scattered, silvery setae; legs with sparse, silvery setae, calcaria whitish; abdominal terga 1–2 with scattered, erect, moderately long, silvery setae, 2 also with moderately dense, long recumbent setae, black except a narrow silver band apically; tergum 3 with scattered, erect, moderately long, scattered, silvery setae, and a narrow apical band of recumbent silvery setae; terga 4–5 with scattered, erect, black setae, 4 with a narrower fringe of recumbent silvery setae than 3; tergum 6 with erect black setae anterolaterally.

Head (Fig. 4) including eyes  $1.2\times$  as wide as thorax; mandible without small, subapical tooth on inner margin (Fig. 1); antennal scrobe with a weak carina; antennal tubercles separated by a distance about the diameter of a tubercle; distance between posterior margin of eye and posterolateral angle of head equal to greatest eye diameter; gena carinate posteriorly (Fig. 3); hypostomal carina not dentate; front and vertex densely punctate, gena moderately so.

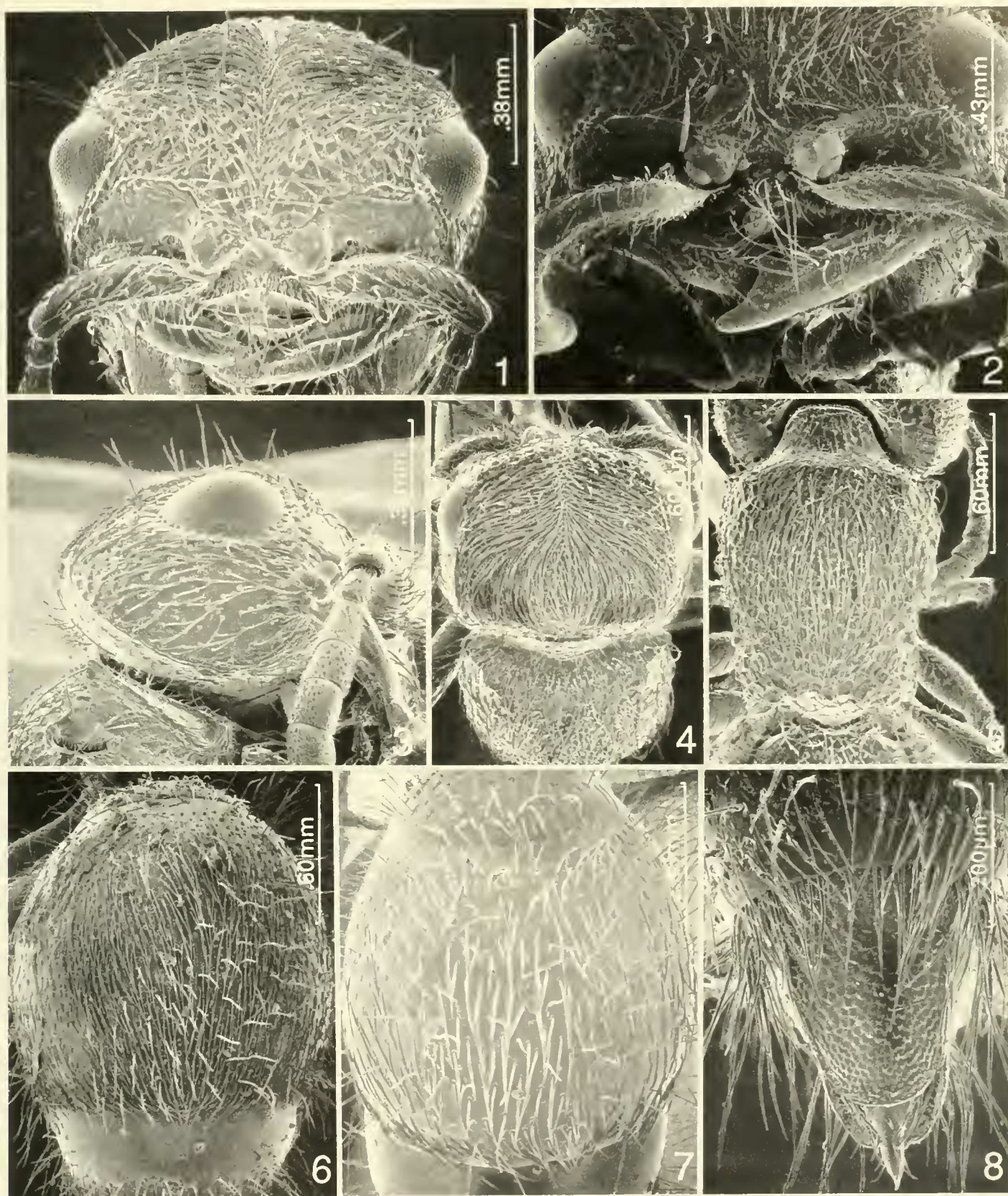
Thorax (Fig. 5) dorsally as wide as long, rather densely punctate on anterior three-fourths, coarsely reticulate posteriorly; humeral angle with small, blunt tooth; side of thorax smooth and polished, mesopleuron anteriorly with vertical carina extending from dorsum to mid coxa; posterior surface of propodeum above with a row of weak, large reticulations, smooth elsewhere, lateral margin carinate but not denticulate.

Second tergum with small separated punctures; pygidium (Fig. 8) carinate laterally on basal half, surface smooth, weakly alutaceous.

Male.—Unknown; possibly similar to *Ps. toumeyii* (Fox) in being 3–5 mm long and having predominantly erect, silvery setae.

Holotype.—ARIZONA: ♀, Cochise Co.,





Figs. 1–8. *Pseudomethoca* species. 1, *perditrix*, head, frontal view. 2, *scaevolella*, head, frontal view. 3, *perditrix*, head, lateral view. 4, *perditrix*, head, dorsal view. 5, *perditrix*, thorax, dorsal view. 6, *scaevolella*, abdominal tergum 2. 7, *perditrix*, abdominal tergum 2. 8, *perditrix*, pygidium.

AZ 82, 0.5 mi W of AZ 90, [4415 ft, on a narrow red dirt road a hundred feet from AZ 82], 4 September 1990, K. V. Krombein (USNM).

Paratypes.—NEW MEXICO: ♀, Hidalgo Co., Animas, [4405 ft], 3 Sep 1990, K.V. Krombein, [on bare earth along NM Route 338] (USNM). ♀, Hidalgo Co., 2 mi N of



Rodeo, [4360 ft], 3 Sep 1989, B. N. Danforth, in nest PPO#11 of *Perdita portalis* Timberlake (KU); ♀, same locality as preceding but 21 Aug 1989, possibly from nest of *Pe. portalis*, B. N. Danforth, (ESB). ARIZONA: ♀, Cochise Co., 17.5 mi SW of Apache, [4120 ft], 25 Jul 1969, K. C. Rozen (AMNH); ♀, Cochise Co., Geronimo Trail, 5.5 mi E of Douglas, [4360 ft], 28–29 Aug 1986, K. V. Krombein (USNM).

Variation.—Paratype females are 3.7–4.5 mm long. The ferruginous is lighter in some specimens, the second abdominal tergum may be slightly darker posterolaterally, and occasionally the femora and tibiae may be red.

Etymology.—From the Latin *perditrix*, destroyer.

Behavior.—Danforth (1991) had a below-ground observation nest of *Perdita portalis* Timberlake, a ground-nesting communal bee, 2 km north of Rodeo. He noted that a cell had been provisioned on 29 August 1989, and saw a female *portalis* in the nest on the 30th. He observed a female *perditrix* on the 31st resting in a filled lateral burrow about 9 cm from the junction with the main tunnel, but saw no bees in the nest that day. The mutillid remained in the nest for four days,<sup>1</sup> and was captured when it left the nest. During those four days the mutillid entered four cells with bee larvae and parasitized three of them. Two post defecating mutillid larvae had spun cocoons by 14 September, and were kept for rearing when the entire observation nest was brought to the laboratory and disassembled. These diapausing larvae were kept at room temperature, and were still viable in November 1991.

<sup>1</sup> This observation confirms Brothers' (1972) supposition that females of *Ps. frigida* (Smith) probably remain for some time in the nest of the host bee. This behavior is perhaps normal when a female *Pseudomethoca* finds a multicellular host nest with brood in various developmental stages, as evidenced also by Norden's finding of two *Ps. bethae* females remaining overnight in a nest of *Exomalopsis solani* Cockerell.

Danforth excavated another *portalis* nest on 21 August 1989. He found a female *perditrix* crawling on the excavated soil, but was not certain whether it came from the nest or was in the immediate vicinity and crawled onto the spoil heap.

The holotype has rather numerous pollen grains over most of the body, particularly around the mouthparts and legs, and some mud adhering to the posterior terga, conditions that suggested she had recently been in the nest of a bee.

*Pseudomethoca toumeyi* (Fox)

Figs. 9, 10

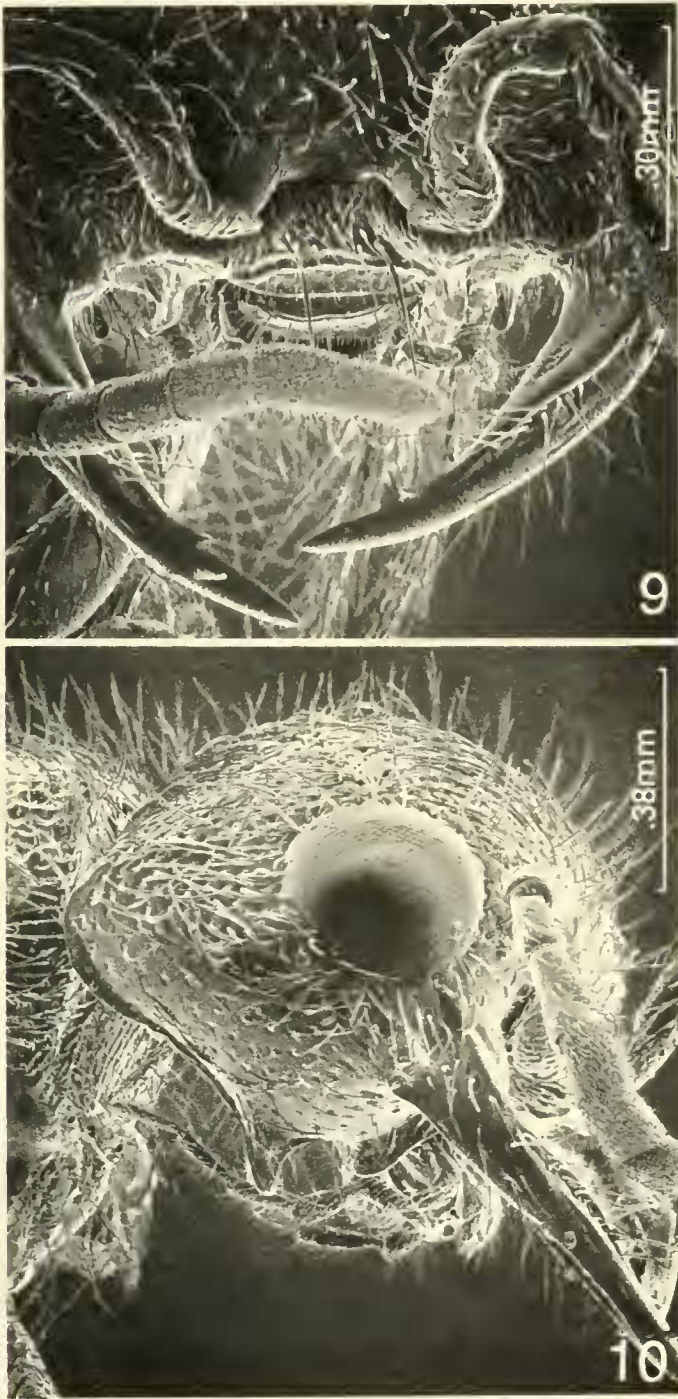
This small species, 3–5 mm long, appears to be the most common taxon of *Pseudomethoca* in southeastern Arizona. A combination of the prominent, acute genal tooth, genal carina extending upward onto the vertex and rounded hypostomal prominence (Fig. 10), the small, acute subapical tooth (occasionally eroded by wear) on the inner margin of the mandible (Fig. 9), and the dense, appressed silvery vestiture on the head and on paired spots on the second abdominal tergum readily separate *toumeyi* from other known species of the genus.

NEW MEXICO: Hidalgo Co., 2 km N of Rodeo, 26 Aug 1989, B. N. Danforth (ESB).

Behavior.—Danforth collected this female crawling on soil excavated from a nest of *Perdita portalis* Timberlake. The *Ps. toumeyi* may have been in the bee's burrow or on the soil surface adjacent to the nest. There were no pollen grains on the mutillid's body.

B. B. Norden collected six female *Ps. toumeyi* (USNM) on the ground at Willcox, Cochise Co., AZ, 24–25 Aug 1990. Some of the mutillids explored nest burrows of the nyssonid wasp, *Hapalomellinus albitomentosus* (Bradley), a species that was preying upon immature cicadellids. The *toumeyi* left the burrows a few seconds after entering them, too short a time for them to have parasitized the wasp larvae. No small bees were nesting in the restricted area where the *toumeyi* were crawling. The mutillids ap-



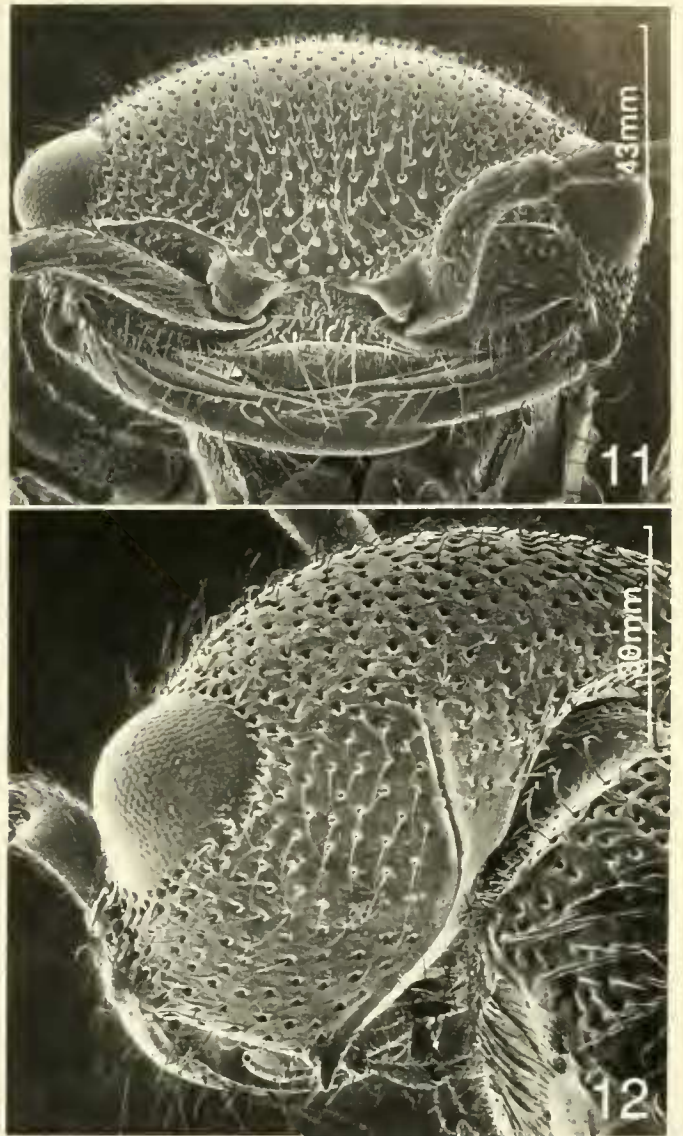


Figs. 9, 10. *Pseudomethoca toumeyi*. 9, mandibles and clypeus. 10, head, lateral view.

peared to be newly emerged, and none bore pollen grains.

*Pseudomethoca torrida* Krombein  
Figs. 11, 12

This is another small species in the 3–5 mm range, and the only small *Pseudomethoca* occurring in peninsular Florida. It is separated from the other species discussed in this paper by a combination of the small, acute genal tooth and genal carina extending



Figs. 11, 12. *Pseudomethoca torrida*. 11, head, frontal view. 12, head, lateroposterior view.

onto the vertex (Fig. 12), and the blunt subapical tooth on the inner margin of the mandible (Fig. 11).

Behavior.—Beth Norden and I were at the Archbold Biological Station, Lake Placid, Florida, 8–15 Aug 1989. We studied the mating behavior and nesting of a solitary andrenid bee, *Perdita graenicheri* Timberlake, a species that constructs a multicellular nest. A number of nest entrances of this gregarious bee were in close proximity in sandy soil near the shore of Lake Annie. No other bees nested nearby. While excavating several nests, Norden collected a female *torrida* crawling on the sand only a few cm distant from *Perdita* nest entrances. I presume that *graenicheri* may be a host of *tor-*



*rida*, a supposition strengthened by the fact that *perditrix*, and perhaps *toumeyii*, are also associated with a species of *Perdita*.

*Pseudomethoca frigida* (Smith)

Behavior.—This species has been reported by many observers (Table 1) as having various small species of halictine bees as positive or putative hosts. *Dialictus zephyrus* (Smith) was noted as a positive or putative host by five observers. In addition, J. C. Bridwell has a double mount of a ♀ *frigida* and ♀ *zephyrus* (USNM), with a note that they were fighting at dusk at a nest entrance at Clifton, VA, 1 July 1933.

There is an anomalous record of a female *frigida* and 5 ♀, 6 ♂ of the eumenid wasp, *Ancistrocerus luttonidus* Bohart emerging from a mud nest (Fattig 1943). Fattig observed a female *luttonidus* bringing mud to her nest “during early May 1929.” The nest was “on a wire lying loosely through the branches of a trailing rose.” He captured the wasp after it made several trips to gather mud, sent it subsequently to G. A. Sandhouse, who identified it as *A. birenimaculatus* (Saussure), a name applied erroneously to the taxon now known as *luttonidus*. Fattig returned “a few weeks later” and found the wire and nest lying on the ground. He removed the nest, placed it in a wire mesh cage, and obtained the series of *luttonidus* and the *frigida*.

I queried Fattig about this host record in 1953. He stated that not all of the mud cells were completed when he recovered the nest, and that C. E. Mickel had identified the *frigida*. Fattig gave his collection to H. O. Lund, University of Georgia, but the nest cannot now be found in the material at the university.

I believe that the association of *frigida* with this eumenid wasp is so unlikely, that a host relationship must be considered improbable. The wasps must have emerged soon after Fattig placed the nest in the cage, because adult emergence of the eumenid would have been expected about a month

after the egg was laid; Fattig picked up the nest “a few weeks” after collecting the mother. Considering the number of confirmed host associations of *frigida* with various halictine bees, I suspect that this particular female had no relationship with the eumenid wasp other than that of just sheltering in an uncompleted cell after the wasp’s nest came into contact with the ground.

I noted (1951) that females of *frigida* and a few males fed on honeydew droppings of the tulip-tree scale on the ground beneath the trees, and that other males visited the secretions on the leaves. Brothers (1972) noted that *frigida* females in sealed observation nests sometimes lapped up liquid from moist pollen-nectar masses in host cells, and that one female punctured a bee pupa with her mandibles and fed on the exuding liquid.

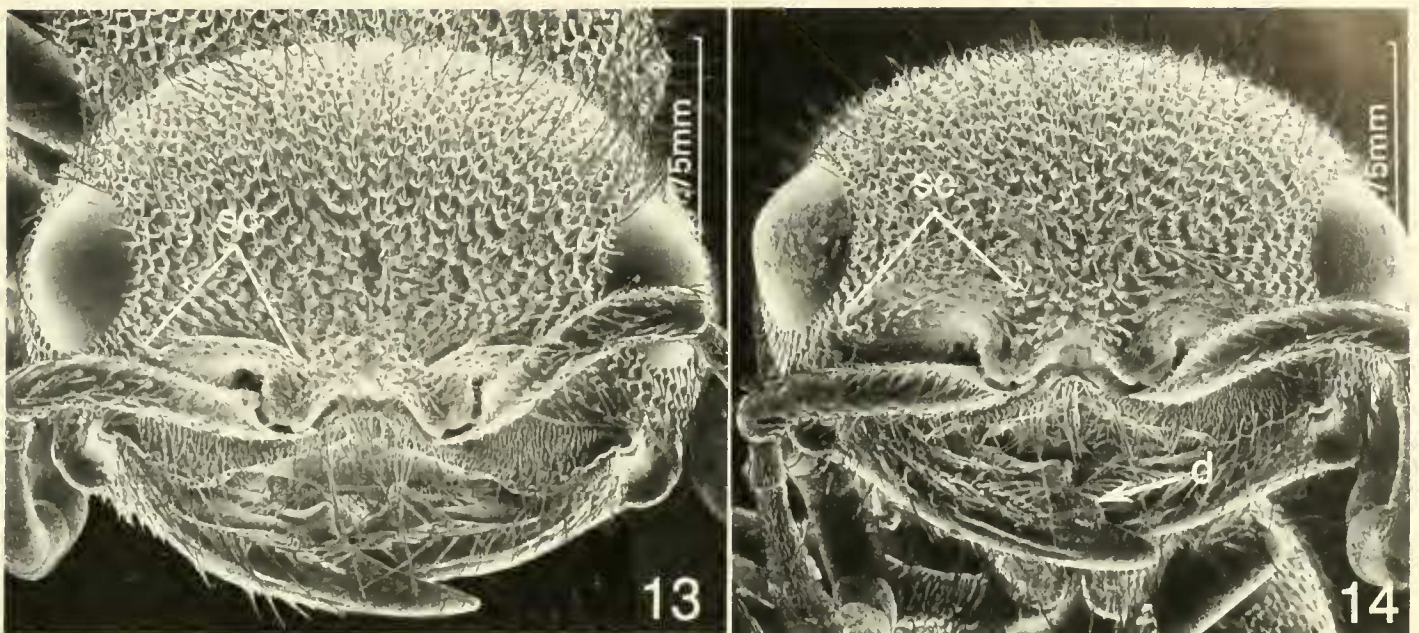
*Pseudomethoca bethae* Krombein,  
NEW SPECIES

Figs. 13–17, 19, 21, 23, 25

In describing *Ps. mulaiki*, Mickel (1938) mentioned that it was distinguished from other species of the genus in America north of Mexico by the pair of pale integumental spots posteriorly on abdominal tergum 2. The present species also has such pale integumental spots, is closely related to *mulaiki*, but differs in a number of details. The two species occupy discontinuous ranges, *mulaiki* being known only from Cameron and Hidalgo counties in extreme southern Texas at low elevations, and *bethae* from the high desert of southeastern Arizona and southwestern New Mexico at 4360–4380 ft elevation, and the Sierra Madre Occidentale of Mexico at elevations of 3600–6000 ft.

The morphological differences are: the carina of the antennal scrobe is weaker and of the same width in *mulaiki*, stronger and noticeably widened proximad in *bethae* (cf. Figs. 13, 14, 19, 20); the antennal tubercles in *mulaiki* are separated from each other by about the diameter of a tubercle, but in *bethae* they are separated by 1.25× their di-





Figs. 13, 14. *Pseudomethoca* species. 13, *bethae*, head, frontal view (sc, scrobal carina). 14, *mulaiki*, head, frontal view (sc, scrobal carina; d, dirt on mandible, not a tooth).

ameter; the hypostomal carina is well developed in both, but it is noticeably higher in *bethae* where it diverges toward the mandible and is not so raised in *mulaiki* (cf. Figs. 21, 22); the vertical mesopleural carina in *mulaiki* extends from the anterior mesonotal tubercle downward to the anterior angle of the midcoxa, but is absent on the lower half or two-thirds in *bethae* (cf. Figs. 23, 24). The pale integumental spots on tergum 2 are ovate and oblique in *mulaiki*, subcircular in *bethae*. There are also differences in the vestiture: the apical fringe of setae on tergum 1 is completely silvery in *bethae*, but black on the middle third in *mulaiki*; and the silvery appressed setae on the pale yellow spots of tergum 2 are connected above by a narrow band of silvery setae in *mulaiki*, but this area in *bethae* has only appressed black setae.

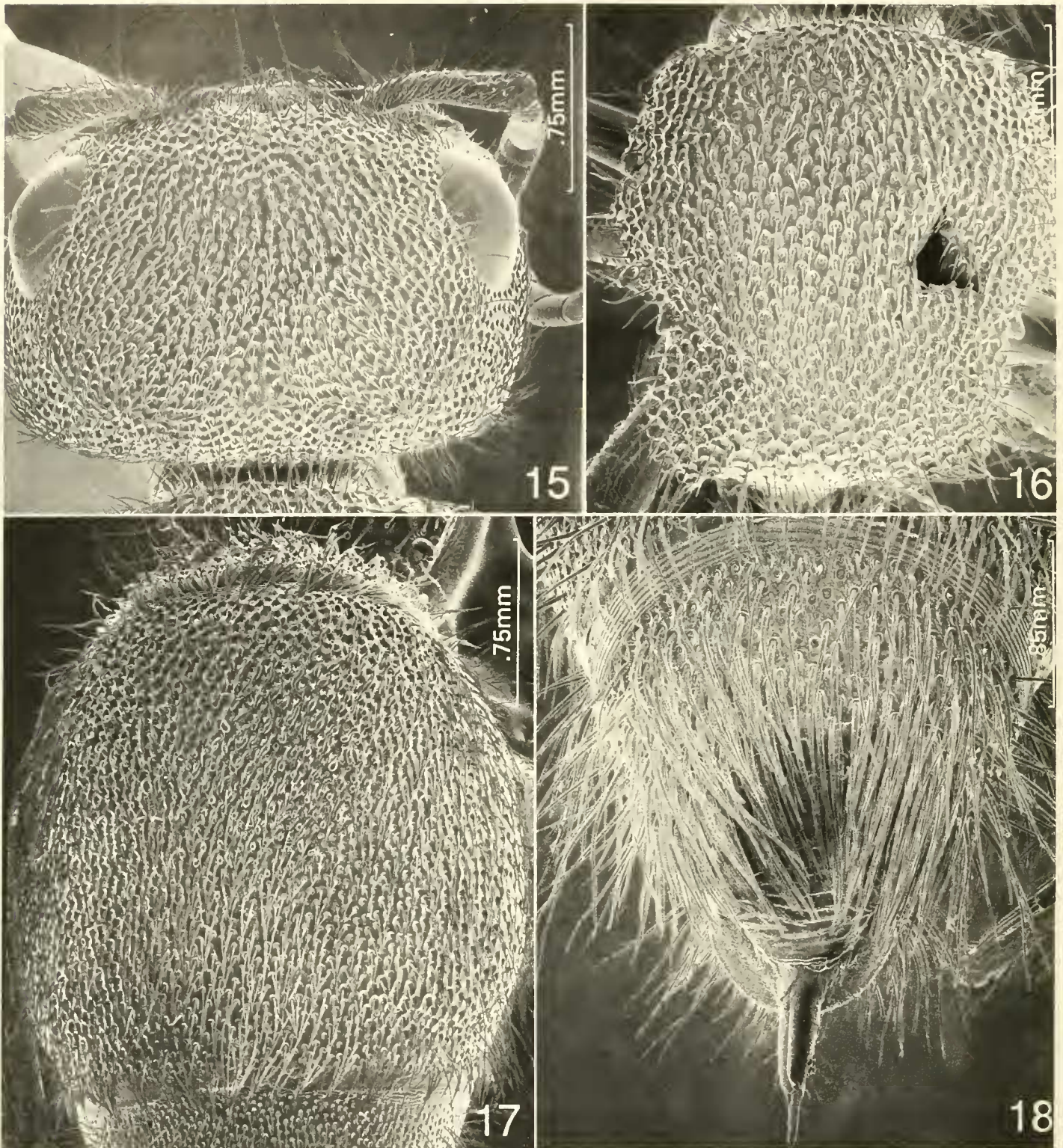
Holotype female.—Length 8.3 mm. Ferruginous, apical half of mandible and antennal flagellum black, the following brown—side of head and large triangular area posterolaterally on top of head; most of abdominal tergum 2 except central spot at base, sides and apex narrowly red, and a pair of moderately large, subcircular, creamy spots toward apex separated from each oth-

er by about their transverse diameter; most of terga 3–6 and apices of sterna; legs mostly darker red than thorax, tarsi paler.

*Vestiture*: Front and vertex with short, rather sparse, subappressed, dark red setae and scattered, longer, erect setae; gena with short, sparser, appressed silvery setae; thoracic dorsum with moderately dense, subappressed reddish setae and scattered, longer, erect silvery setae; terga 1–5 with a band of appressed silvery setae, that on 1 wider except narrowly in middle, 2–5 quite narrow, rather inconspicuous on 4–5; tergum 1 with small subapical patch of black setae; tergum 2 with dense appressed setae, silvery on pale yellow spots and on a narrow, vaguely defined strip extending anteriorly from each pale spot and becoming slightly broader toward base of tergum, black on darker areas, and with scattered, longer, erect silvery setae; 3–5 with scattered, erect silvery setae anteriorly; 6 with coarse, dense, subappressed pale setae on basal half (Fig. 18); sterna 2–5 with scattered, longer, suberect silvery setae anteriorly and a narrow apical band of subappressed silvery setae; sternum 6 with erect silvery setae; legs with sparse, silvery pubescence, calcaria pale.

Head (Fig. 15) including eyes  $1.1 \times$  as wide



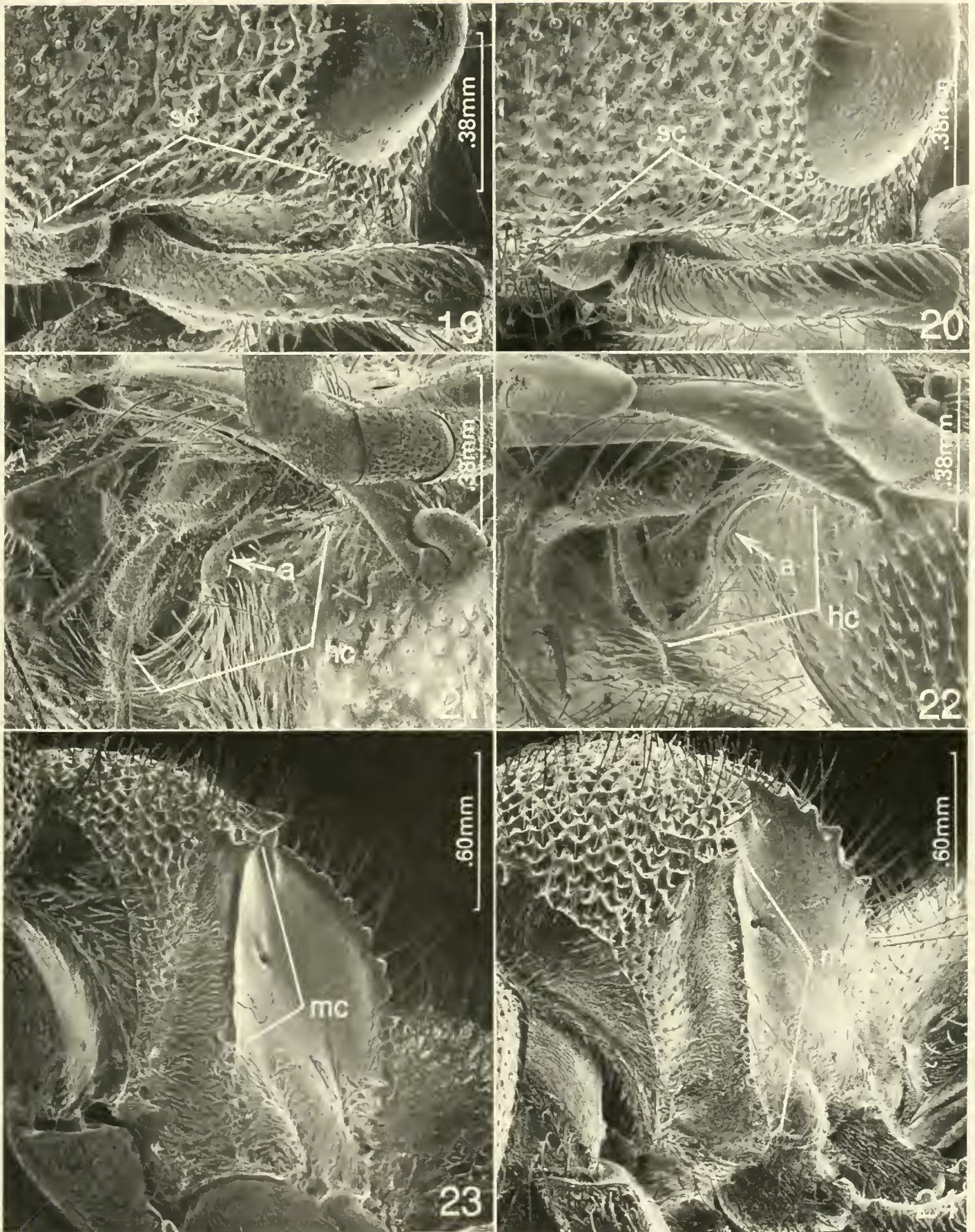


Figs. 15–18. *Pseudomethoca bethae*. 15, head, dorsal view. 16, thorax, dorsal view. 17, abdominal tergum 2. 18, pygidium.

as thorax; mandible as in *mulaiki*, with a large tooth at midpoint of inner margin, and a tiny tooth halfway between tip and large tooth, teeth sometimes obscured by long setae curving downward from base of clypeus and inward from mandible (Fig. 13); antennal scrobe with a strong carina noticeably

higher proximad (Fig. 19); antennal tubercles separated by about  $1.25 \times$  the diameter of a tubercle; distance between posterior margin of eye and posterolateral angle of head equal to greatest diameter of eye; gena carinate posteriorly; hypostomal carina well developed, not dentate but noticeably high-





Figs. 19–24. *Pseudomethoca* species. 19, *bethae*, left side of head, dorsal (sc, scrobal carina). 20, *mulaiki*, left side of head, dorsal (sc, scrobal carina). 21, *bethae*, underside of head, oblique (hc, hypostomal carina; a, angle). 22, *mulaiki*, underside of head, oblique (hc, hypostomal carina; a, angle). 23, *bethae*, side of thorax, oblique from anteriorly (mc, mesopleural carina). 24, *mulaiki*, side of thorax, oblique from anteriorly (mc, mesopleural carina).





Fig. 25. *Pseudomethoca bethae*, head, frontal view showing extreme mandibular erosion.

er where it diverges toward mandible than in *mulaiki* (cf. Figs. 21, 22); front and vertex with dense punctures, those on gena more separated.

Thorax dorsally (Fig. 16) as wide as long, widest at anterior mesonotal tooth, densely punctate becoming reticulate apically; humeral angles carinate but not produced; side of mesonotal area with a pair of teeth, anterior one above vertical mesopleural carina; lateral surface of pronotum carinate anteriorly; vertical mesopleural carina (Fig. 23) extending from dorsum only halfway toward anterior angle of midcoxa, a more delicate oblique carina extending from posterior angle of midcoxa to lower end of vertical carina; posterior surface of propodeum narrowly reticulate above and laterally, finely scattered punctures below, lateral margin denticulate.

Tergum 2 (Fig. 17) closely punctate, more deeply and densely anteriorly than laterally and apically; tergum 6 (Fig. 18), pygidial

area with transverse, somewhat irregular rugulae, not carinate laterally.

Male.—Unknown.

Holotype.—NEW MEXICO: ♀, Hidalgo Co., 3 km N of Rodeo, [4360 ft], 24 Aug 1991, B. B. Norden (USNM).

Paratypes.—NEW MEXICO: ♀, same label data as holotype except 25 Aug 1991; ♀, same label data as holotype except 2 km N of Rodeo, 21 Aug 1991, K. V. Krombein; ♀, Rodeo, 31 Aug 1970, D. J. Brothers (DJB); ARIZONA: 2 ♀, Cochise Co., Apache, [4380 ft], 30 Aug–1 Sep 1986, K. V. Krombein (USNM). 3 ♀, same locality but 27–31 Aug 1988, K. V. Krombein, B. Norden (USNM); 2 ♀, same locality but 31 Aug 1988, B. Norden, one in nest gallery and one in cell of *Exomalopsis solani* Cockerell; ♀ MEXICO, Jalisco, south edge of Guadalajara, 6000 ft, 11 Jul 1973, R. R. & M. E. Murray (DGM); ♀, MEXICO, Puebla, 11 km NW Tehuiztzingo, 1100 m, 1–2 Jul 1975, E. M. & J. L. Fisher (DGM).



The holotype and 21 Aug 1991 paratype are newly emerged females in pristine condition.

Variation.—The tiny tooth on the inner margin of the mandible halfway between the tip and the large tooth may be lacking, possibly having been eroded by use. One paratype from the nest at Apache has such badly eroded mandibles (Fig. 25), apparently from digging into the cement-like bee cells, that the tips do not meet on the midline and the large tooth on the inner margin is entirely worn off. The paratypes from New Mexico and Arizona are rather uniform in size, 7.3–8.2 mm long. They agree well with the holotype except the gena and first flagellar segment are red in one specimen, and the flagellum and apex of the mandible are brown in another. The Mexican specimens are 5.5 (Puebla) and 9.5 mm long (Guadalajara) and differ in a few details of coloration and vestiture as follows: head and legs uniformly red; vertex with either a median area or entirely with appressed black setae; appressed setae of thoracic dorsum entirely black or only in the middle; darker areas of tergum 2 lighter in hue; and apical fringe of tergum 2 black except extreme side in Puebla specimen.

Discussion.—*Ps. bethae* and *mulaiki* belong to a complex of species occurring in Mexico and Central America that is characterized by the pair of pale integumental spots posterolaterally on tergum 2, and the thorax noticeably narrowed posteriorly with a pair of prominent teeth laterally on the mesonotum. Several of the species also share with *bethae* the similarly developed antennal scrobe and hypostomal carina but are otherwise distinct. Cameron (1894–1900) described two species from Mexico in *Sphaerophthalma* (sic) that may belong to the complex but they are not *bethae*.

Etymology.—The species is named for Beth B. Norden, a cherished companion in the field, discoverer of the species' host, and, most recently, collector of the holotype.

Behavior.—Norden began to excavate a

nest of the communal anthophorid bee, *Exomalopsis solani* Cockerell, at noon on 30 August. She found a female *bethae* under a rock near the nest entrance, and also collected several *solani* bearing pollen as they returned to the nest. By the end of the day Norden had exposed the perpendicular main tunnel and reached a depth of about 40 cm. She stuffed grass tightly into a section of the main burrow to prevent egress or ingress. We then placed a large rubberized poncho in the bottom of the pit and against the vertical, exposed burrow profile, folded the top of the poncho over the level ground surface, and placed rocks and loose soil on the edge of the poncho. We then filled the excavation with the loose soil that had been removed earlier.

After removing the loose soil and poncho, and finding the plug of grass still intact in the main tunnel Norden continued the excavation at noon on the 31st. She found a female *bethae* at the 37 cm level on the pollen-nectar mass in an uncompleted bee cell apparently feeding on the moist mass. This substantiates Brothers' (1972) observation of *Ps. frigida* feeding on a pollen-nectar mass in the host nest.

She found a second female *bethae* with badly eroded mandibles at the 39 cm level in an empty gallery. The mandibles of the female from the 37 cm level also were eroded, but not so badly as in the second specimen. There is no doubt that both females had been in the nest when Norden began the excavation on the 30th because we had thoroughly sealed access to the burrow at the end of that day.

She recovered a number of sealed cells, several of which were parasitized by larvae of other aculeate Hymenoptera. Subsequently she reared several adult *Nomada* (*Micronomada*) *gutierreziae* Cockerell from some of the parasitized cells.

I collected two of the 27–31 August female of *bethae* and two females of *gutierreziae* in an area of about one hectare surrounding the nest location. The variation in



size of the type series of *bethae* indicates strongly that other bees also serve as hosts of this mutillid. I also collected in the same area several specimens of the nomadine bee, *Paranomada nitida* Linsley. It is known to parasitize species of *Exomalopsis*, but was not reared from this nest of *solani*. I have included *gutierreziae* as a questionable host of *bethae* in Table 1 inasmuch as its larva may also serve as a host for the mutillid.

Several *bethae* from Apache and the Jalisco specimen, all captured while crawling on the ground, have grains of pollen around the mouthparts, indicating that they had recently been within a bee nest.

Females may be found on sunny days crawling on the ground, once the surface has warmed sufficiently, from about 0900 h until 1030. Diurnal activity above ground resumes in the late afternoon from about 1600 until at least 1730. Hours of above ground activity may be lengthened during overcast conditions. The three specimens of *bethae* collected on 21, 24 and 25 August 1991 were taken respectively at 0930, 1715 and 1730. We noted similar periods of activity above ground for females of other *Pseudomethoca*, e.g. *perditrix*, *scaevolella*, and *toumeyi*.

*Pseudomethoca mulaiki* Mickel

Figs. 18, 20, 22, 24

Three females (2 in USNM, 1 in DGM) from Bentsen, Rio Grande Park, Hidalgo Co., Texas, agree in all details with Mickel's unique type from N.E. Cameron Co., Texas, off Bird Island, except that the integument of the type is a lighter red.

Behavior.—Two of the Bentsen specimens each bear an additional label, "A. Hook/Bio.Note No./1.42-81/" or "1.43-81." Hook (unpublished notes) was working at Bentsen during 1981 on the nesting and behavior of the philanthid wasp, *Trachypus mexicanus* Saussure, which preys upon other aculeate Hymenoptera, chiefly Apoidea. The prey, taken either in nests or from wasps

in flight, included: Halictidae—*Agapostemon* (10 of one species, 2 each of two others), 1 specimen of *Sphecodes*, 5 specimens of *Dialictus*, and 34 specimens of *Augochlorella*; and Anthophoridae—10 specimens of *Exomalopsis*, and one specimen of *Melissodes*. He noted four species of mutillids, three of *Dasymutilla* and one of *Pseudomethoca*, searching the nesting areas of *T. mexicanus*. He saw five episodes of mutillids halting and retreating from nest entrances of *mexicanus* due to the presence of guards, and eight episodes of mutillids entering inactive nests and remaining inside 10 seconds to 16 minutes. He reared no mutillids from 83 viable cocoons of *mexicanus*.

Hook's two *mulaiki* show only slight wear of the apical mandibular tooth, but no erosion of the large tooth on the inner margin of the mandible. The wear of the apical tooth may have been incurred during the mutillid's exit from the cocoon to the ground surface. Hook thought that nests of many of the bees listed as wasp prey were interspersed among the wasp nests.

*Pseudomethoca propinqua* (Cresson)

Behavior.—I reported *Nomia melanderi* Cockerell as a host of *propinqua* (1958). This was based on two females from Riverton, Wyoming, 14 August 1957, sent for identification by G. F. Knowlton with a note that they parasitized this bee. Knowlton never validated this record by publication of the details, so I consider that it is only a putative association.

Later, I received from W. L. Jellison a copy of a letter that he had written to C. E. Mickel concerning enormous populations of female bees, and of a mutillid which Mickel identified subsequently as *propinqua*. Jellison stated that he had observed both species early in August 1971, shortly after their appearance on a bare, level, rather sandy lot of about 6500 sq ft in Ravalli Co., Montana. Thousands of the bees were burrowing in the soil. He estimated 6000–



7000 *propinqua* males in sight at one time, and that females outnumbered males by 10:1. He noted that *propinqua* males were swarming when it was cool, but scarce when it got hot, and that they flew swiftly just above the ground surface. He also saw 4–5 males clustered around a single female, but did not mention seeing mating. He stated that “other bees (possibly parasites), wasps and tiger beetle larvae” were in the area. Although he visited the site on three successive dates, he did not mention seeing *propinqua* females entering bee burrows. There is a tray of material from Jellison with the above locality and date labels in the USNM *Pseudomethoca* collection. It contains 5 ♀ and 11 ♂ *propinqua*, and the following anthophorid bees identified by P. D. Hurd, Jr.: 4 ♀ *Melissodes* (*Eumelissodes*) *pallidisignata* Cockerell and 4 ♀ *Triepeolus wyomingensis* Cockerell.

Knowlton's *propinqua* are somewhat smaller than Jellison's specimens, a size difference that is also evident in the three putative bee hosts. None of the *propinqua* bear pollen grains around the mouthparts, indicating that they had not been feeding on the pollen-nectar masses within bee nests, at least recently. Knowlton's specimens do not have worn mandibles nor is there mud on the tibiae. One of Jellison's specimens has the mandibles quite worn, and three evidence some mandibular wear; three have some mud on the mid and hind tibiae, an indication that they had been exploring burrows. All of the *pallidisignata* had been gathering pollen, so provisioning of nests was in progress. It seems probable that *pallidisignata* was the host of *propinqua* considering the very large populations of each, the absence of large numbers of any other bee species, and the relative sizes of the individuals.

There is a possibility that *wyomingensis* also may have *pallidisignata* as a host, in which case a mature larva of the *Triepeolus* in a *pallidisignata* cell could also conceivably serve as a host of *propinqua*.

*Pseudomethoca sanbornii sanbornii*  
(Blake)

Mickel (1924) reported that both sexes of this taxon were reared by E. A. Schwarz from cells of the halictid bee, *Nomia pattoni* Cockerell, from Selma, Alabama.

*Pseudomethoca sanbornii aetis* (Fox)

Behavior.—D. G. Manley advised me that he found a number of females of this mutillid crawling on the ground among a large aggregation of nests of the solitary halictid, *Nomia nevadensis bakeri* Cockerell. The nests were in a fallow, cultivated field in coastal South Carolina. He did not observe female mutillids entering the nests, but the large numbers of both populations suggest a probable host-parasite association. This probable host association is strengthened by the fact that nominotypical *Ps. sanbornii* (Blake) was reared from cells of *Nomia pattoni* Cockerell.

Beth Norden (Krombein and Norden, in preparation) collected one female visiting exudate from a fruiting stalk of a scrub palmetto in Florida. The fluid was obtained from a wound made by a *Dasymutilla* female at the base of the fruit bearing stem.

*Pseudomethoca donaeanae*  
(Cockerell and Fox)

The species has a wide distribution in the desert from western Texas to southern California. Mickel (1924, 1935) did not describe it other than to give key characters, and he did not mention the size. The single female in USNM is 8.0 mm long, has an untoothed genal carina, mandible with two teeth along the inner margin, a strongly developed scrobal carina, and a well developed median tubercle at the apex of the thoracic dorsum.

ARIZONA: Cochise Co., Apache, [4380 ft], 30 Aug–1 Sept 1986, K. V. Krombein.

Behavior.—This female was crawling on the ground where various aculeate Hymenoptera were nesting. The mandibles were



quite unworn, suggesting that it had emerged recently. There were numerous pollen grains on the venter of the head and mandibles, and fewer scattered grains elsewhere on the head, thorax and abdomen, evidence that it had fed recently on a pollen-nectar mass in a bee nest.

#### HOST ASSOCIATIONS OF *PSEUDOMETHOCA*

A review of the positive and putative host associations of *Pseudomethoca* from America north of Mexico as listed in Krombein (1979), from subsequent literature and in the present contribution, suggests that solitary and communal bees may be the only hosts within the genus. Forty-five species-level taxa are now known from this area, 17 from both sexes, 20 from females only, and 8 from males only. Fourteen species-level taxa (31%) have bees as positive or putative hosts as listed in Table 1. If we assume, as is probable, that the eight species known from males only are the opposite sexes of taxa presently known only from females, the taxa with possible bee hosts increases to 38%.

There are a number of *Pseudomethoca* species, mostly undescribed, in Central and South America. There are positive host records for three species from Costa Rica and Panama. Mickel (1969) described *Ps. willei* from specimens reared from cells of the halictid, *Dialictus umbripennis* (Ellis), in Costa Rica. Brooks and Roubik (1983) reported *Ps. hesperus* Brothers and *Ps. transversa* Brothers as parasitoids of the halictid bee, *Halictus (Seladonia) hesperus* Smith. Specimens of both *Pseudomethoca*, but mostly *hesperus*, were noted trying to enter, or actually entering nests of the bees, but being repelled by guard bees.

I consider positive host associations in *Pseudomethoca* to be actual rearing of the parasitoid from a cell of the host bee, finding a female mutillid ovipositing on a paralyzed host larva, or observing the female mutillid fighting with a guard bee at or near the nest entrance.

A probable host association could be finding a female mutillid in a bee nest, sometimes feeding on the pollen-nectar mass, but no evidence otherwise that there might be a host association.

Another possible host association might be with a parasitic anthophorine bee, such as *Nomada* or *Triepeolus*. Mature or diapausing larvae of these bees could serve as possible hosts of *Pseudomethoca*. Eggs of the parasitic bees are placed in a host bee cell containing a pollen-nectar mass and host bee egg. They usually hatch before the host egg, seek out the latter and destroy it or a newly hatched host larva, before feeding on the pollen-nectar mass. They might be as subject as host bee larvae to parasitism by a mutillid.

Finally, the finding of numerous pollen grains especially on the venter of the head and mandibles, and also sometimes scattered more sparsely on the head, thorax and abdomen of a female *Pseudomethoca* is persuasive, presumptive evidence that the specimen had been feeding at a pollen-nectar mass in a cell of a bee. A lack of pollen around the mouthparts would not eliminate the possibility that the mutillid fed at a pollen-nectar mass, because thorough grooming might remove the pollen. I have noted finding numerous pollen grains on the mouthparts of some specimens in some of the individual accounts that precede this section.

*Pseudomethoca* females have not been reported to visit flowers for nectar. Females of *frigida* and *simillima* were found visiting honey-dew secretions of the tulip-tree scale on the ground (Krombein 1951); probably females may also visit secretions of aphids in similar sites. A female of *sanbornii aetis* was noted on sweet exudate from a scrub palmetto fruit (Krombein and Norden, in preparation).

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Table 1. Host associations in *Pseudomethoca*: an asterisk denotes a positive host association; lack of an asterisk denotes a possible or probable host association; the abbreviations And., Ant., and Hal. are of the host bee families Andrenidae, Anthophoridae, and Halictidae; and question mark, ?, before a name denotes a possible host.

<i>Pseudomethoca</i>	Host Bee	Source
<i>bethae</i> , n. sp.	Ant.: <i>Exomalopsis solani</i> Cockerell. ? <i>Nomada</i> ( <i>Micronomada</i> ) <i>gutierreziae</i> Cockerell	Krombein, supra
<i>donaeanae</i> (Cockerell & Fox)	Unknown bee	Krombein, supra
<i>frigida</i> (Smith)	Hal.: * <i>Dialictus zephyrus</i> (Smith) (recorded as <i>pruinus</i> (Robertson))	Melander & Brues, 1903
	Hal.: * <i>Dialictus zephyrus</i> (Smith)	Krombein, 1938
	Hal.: <i>Augochlorella striata</i> (Provancher)	Michener & Wille, 1961
	Hal.: * <i>Dialictus zephyrus</i> (Smith)	Lin, 1964
	Hal.: * <i>Dialictus zephyrus</i> (Smith)	Batra, 1965, 1966
	Hal.: * <i>Dialictus versatus</i> (Robertson)	Michener, 1966
	Hal.: * <i>Evyllaesus cinctipes</i> (Provancher)	Knerer & Atwood, 1967
	Hal.: * <i>Dialictus zephyrus</i> (Smith), * <i>D. coeruleus</i> (Robertson), <i>D. imitatus</i> (Smith), <i>D. laevis</i> (Smith), <i>D. rohweri</i> (Ellis)	Brothers, 1972
<i>gila</i> (Blake)	Andrenidae: <i>Pseudopanurgus rugosus</i> (Robertson)	Manley and Neff, 1989
<i>mulaiki</i> Mickel	Hal.: <i>Agapostemon angelicus</i> Cockerell, <i>A. melliventris</i> Cresson, <i>A. texanus</i> Cresson Ant.: <i>Exomalopsis</i> sp.	Krombein, supra
<i>nudula</i> Mickel	And.: ? <i>Calliopsis</i> sp.	Mickel, 1924
<i>perditrix</i> , n. sp.	And.: * <i>Perdita portalis</i> Timberlake	Krombein, supra
<i>propinqua</i> (Cresson)	Hal.: <i>Nomia melanderi</i> Cockerell Ant.: <i>Melissodes</i> ( <i>Eumelissodes</i> ) <i>pallidisignata</i> Cockerell, ? <i>Triepeolus wyomingensis</i> Cockerell	Krombein, 1958 Krombein, supra
<i>sanbornii sanbornii</i> (Blake)	Hal.: <i>Nomia pattoni</i> Cockerell	Mickel, 1924
<i>sanbornii aetis</i> (Fox)	Hal.: <i>Nomia nevadensis bakeri</i> Cockerell	Krombein, supra
<i>simillima</i> (Smith)	And.: * <i>Andrena macra</i> Mitchell Ant.: * <i>Nomada</i> sp.	Riddick, 1991
<i>torrida</i> Krombein	And.: <i>Perdita graenicheri</i> Timberlake	Krombein, supra
<i>toumey</i> (Fox)	And.: <i>Perdita portalis</i> Timberlake	Krombein, supra
<i>vanduzeei</i> Bradley	Hal.: * <i>Nomia maneei</i> Cockerell	Fattig, 1943

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#### LITERATURE CITED

- Batra, S. W. T. 1965. Organisms associated with *Lasioglossum zephyrum* (Hymenoptera: Halictidae). *Journal of the Kansas Entomological Society* 38: 367-389.
- . 1966. The life cycle and behavior of the primitively social bee, *Lasioglossum zephyrum* (Halictidae). *University of Kansas Science Bulletin* 46: 359-422.
- Brooks, R. W. and D. W. Roubik. 1983. A halictine bee with distinct castes: *Halictus hesperus* (Hymenoptera: Halictidae) and its binomics in central Panama. *Sociobiology* 7: 263-282.
- Brothers, D. J. 1972. Biology and immature stages of *Pseudomethoca f. frigida*, with notes on other species (Hymenoptera: Mutillidae). *University of Kansas Science Bulletin* 50: 1-38.
- Cameron, P. 1894-1900. Mutillidae in *Biologia Centrali-Americana*, Hymenoptera 2: 259-395, pls. 13-14.
- Danforth, B. N. 1991. Female Foraging and Intra-nest Behavior of a Communal Bee, *Perdita portalis* (Hymenoptera: Andrenidae). *Annals of the Entomological Society of America* 84: 537-548.
- Fattig, P. W. 1943. The Mutillidae or Velvet Ants of Georgia. *Emory University Museum Bulletin* 1. 24 pp.
- Knerer, G. and C. E. Atwood. 1967. Parasitization of social halictine bees in southern Ontario. *Proceedings of the Entomological Society of Ontario* 97: 103-110.
- Krombein, K. V. 1938. Notes on the biology of *Pseudomethoca frigida* (Smith) (Hymenoptera: Mutillidae). *Bulletin of the Brooklyn Entomological Society* 33: 14-15.
- . 1951. Wasp visitors of tulip-tree honeydew at Dunn Loring, Virginia (Hymenoptera Aculeata). *Annals of the Entomological Society of America* 44: 141-143.
- . 1958. Genus *Pseudomethoca* Ashmead, p. 103. *In* Hymenoptera of America north of Mexico, First Supplement.
- . 1979. Genus *Pseudomethoca* Ashmead. *In* Krombein et al., *Catalog of Hymenoptera in America north of Mexico*, vol. 2: 1301-1304.
- Krombein, K. V. and B. B. Norden. (In preparation). Above-ground feeding of North American mutillid females (Hymenoptera: Mutillidae).
- Lin, C. S. 1964. Increased parasitic pressure as a major factor in the evolution of social behavior in Halictine bees. *Insects Sociaux* 11: 187-192.
- Manley, D. G. and J. L. Neff. 1989. *Pseudomethoca ilione* (Fox), a new synonym of *P. gila* (Blake) (Hymenoptera: Mutillidae). *Pan-Pacific Entomologist* 65: 12-14.
- Melander, A. L. and C. T. Brues. 1903. Guests and parasites of the burrowing bee *Halictus*. *Biological Bulletin* 5: 1-27.
- Michener, C. D. 1966. The bionomics of a primitively social bee, *Lasioglossum versatum* (Hymenoptera: Halictidae). *Journal of the Kansas Entomological Society* 39: 193-217.
- Michener, C. D. and A. Wille. 1961. The bionomics of a primitively social bee, *Lasioglossum inconspicuum*. *University of Kansas Science Bulletin* 42: 1123-1202.
- Mickel, C. E. 1924. A revision of the mutillid wasps of the genera *Myrmilloides* and *Pseudomethoca* occurring in America north of Mexico. *Proceedings of the United States National Museum*, 64, Art. 5. 51 pp.
- . 1935. Descriptions and records of Mutillid wasps of the genera *Myrmilloides* and *Pseudomethoca* (Hymenoptera: Mutillidae). *Transactions of the American Entomological Society* 61: 383-398.
- . 1938. Synonymical notes and new species of *Pseudomethoca* and *Dasymutilla* (Mutillidae: Hymenoptera). *Annals of the Entomological Society of America* 31: 147-156.
- . 1969. *Pseudomethoca willei*, n. sp., reared from cells of the bee *Lasioglossum (Dialictus) umbripennis* (Ellis). *Journal of the Kansas Entomological Society* 42: 524-526.
- Riddick, E. W. 1991. *Pseudomethoca simillima* (Smith) (Hymenoptera: Mutillidae), a newly discovered parasitoid of *Andrena macra* Mitchell (Hymenoptera: Andrenidae). *Proceedings of the Entomological Society of Washington* 93: 208-209.